

Climate change alterations to ecosystem dominance: how might sponge-dominated reefs function?

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Abstract. Anthropogenic stressors are impacting ecological systems across the world. Of particular concern are the recent rapid changes occurring in coral reef systems. With ongoing degradation from both local and global stressors, future reefs are likely to function differently from current coral-dominated ecosystems. Determining key attributes of future reef states is critical to reliably predict outcomes for ecosystem service provision. Here we explore the impacts of changing sponge dominance on coral reefs. Qualitative modelling of reef futures suggests that changing sponge dominance due to increased sponge abundance will have different outcomes for other trophic levels compared with increased sponge dominance as a result of declining coral abundance. By exploring uncertainty in the model outcomes we identify the need to (1) quantify changes in carbon flow through sponges, (2) determine the importance of food limitation for sponges, (3) assess the ubiquity of the recently described “sponge loop,” (4) determine the competitive relationships between sponges and other benthic taxa, particularly algae, and (5) understand how changing dominance of other organisms alters trophic pathways and energy flows through ecosystems. Addressing these knowledge gaps will facilitate development of more complex models that assess functional attributes of sponge-dominated reef ecosystems.

Key words: coral reefs; ecosystem functioning; Porifera; qualitative modelling; regime shifts; sponges.

INTRODUCTION

Environmental degradation is having a major impact on marine, terrestrial, and freshwater biomes across the world, altering species distribution patterns, biodiversity, and trophic structure (Estes et al. 2011). Anthropogenic stressors have negatively impacted coral reefs across the world and the rate of degradation does not appear to be abating (De'ath et al. 2012, Hughes et al. 2017a). For example, in 2016 and 2017, the Great Barrier Reef (GBR) in Australia experienced extensive coral bleaching, with over 80% of reefs affected (Hughes et al. 2017b). While there is an increased global effort to sustainably manage and conserve the marine environment, there is also increasing recognition that future reefs are likely to look and function differently to current reefs, including those that are already degraded by local stressors and global climate change (Hughes et al. 2017a). Given the need to effectively manage coral reefs for

their essential ecosystem services such as tourism and fisheries, it is timely to consider how future reef states might function compared to current coral-dominated reef ecosystems and reefs that have existed in recent history.

Changes in either the relative or absolute abundance of reef organisms will likely have flow-on consequences for the function of reef ecosystems. Sponges are important components of coral reefs and there is increasing evidence that many sponges may be more tolerant to the impacts of climate change than corals (Duckworth et al. 2012, Bennett et al. 2017, 2018). While transitions to algal-dominated reefs have been well described (Roff and Mumby 2012), few studies have assessed how these new states may function (but see Graham et al. 2014, McClanahan et al. 2014, Harborne et al. 2017, Hughes et al. 2017b for discussion of the issue) and little is currently known about how reefs dominated by other groups such as filter feeders might function. Here we use qualitative models to explore broad ecosystem-level outcomes from a change to reefs dominated by sponges and identify research gaps to refine our understanding of how these reefs would function. While a number of conceptual and parameterized models have considered current-day sponge trophic

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interactions (Pawlik 2011, de Goeij et al. 2013, Pawlik et al. 2016, McMurray et al. 2017), and one model has considered sponge spatial competition with macroalgae and corals (González-Rivero et al. 2012), no studies have yet explored ecosystem-wide consequences of increased sponge abundance and dominance (Bell et al. 2013).

DIRECT IMPACTS OF SPONGES ON ECOSYSTEM FUNCTION

A shift toward sponge dominance on reefs may occur if sponge abundance/biomass increases through greater utilization of space or increased productivity (Bennett et al. 2017), or if sponges exhibit high environmental resilience leading to a greater relative decline in coral abundance. In recent years there have been numerous reports of transitions toward sponge-dominated states in reefs spanning the Caribbean, Atlantic, Indo-Pacific, and Pacific regions (reviewed in Bell et al. 2013). Given that sponges have many important functional roles on coral reefs (Bell 2008), particularly through their trophic interactions with the water column (Reiswig 1971, 1975, Maldonado et al. 2012, McMurray et al. 2017), shifts toward sponge-dominated ecosystem states would have a number of direct impacts on ecosystem function (Table 1). Many of these direct impacts, such as bioerosion (excavating and boring sponges, e.g., Murphy et al. 2016), picoplankton removal (Morganti et al. 2016), and net primary production (Wilkinson 1983) are relatively easy to quantify, but little is known about the subsequent ecosystem-level consequences of these changes. Importantly, while there has been a considerable focus on sponge feeding interactions and bioerosion on coral reefs, for many of the

other direct impacts, such as nutrient cycling by symbiotic microorganisms, there is generally a paucity of information for tropical systems (Webster and Thomas 2016). Currently, this limits our ability to predict the broader functional consequences of changing sponge abundance on reefs.

Absolute increases in sponge abundance will have direct impacts on the water column through the uptake of particulate organic matter (POM; comprising both living material and detritus) and dissolved organic matter (DOM; Lesser 2006), potentially reducing availability to other organisms. However, at the same time, sponges are also releasing detritus (de Goeij et al. 2013), inorganic nutrients (Ribes et al. 2012), and mucus (McGrath et al. 2017), which may be directly available to other organisms. Most sponges take up both POM and DOM, although the rate of uptake of these different carbon forms likely varies between species, particularly between those harboring high (HMA) or low (LMA) microbial abundances (Morganti et al. 2017). The release of carbon from sponges is likely to be more important than direct consumption of sponges in moving biomass and energy to higher trophic levels, given that there are generally few organisms on reefs that directly feed on sponges (Wulff 2006). Other direct biological impacts of increased sponge abundance include greater levels of spatial competition and, while there is no evidence to suggest that actual sponge competitive ability will increase, the frequency of interactions will likely increase, with negative impacts for inferior competitors (de Voogd et al. 2003). At the same time, increased sponge spatial occupation will reduce the space available for settlement and establishment of other organisms, such as corals. Both absolute and relative changes in sponge abundance are also likely

TABLE 1. Direct ecosystem effects of increasing the abundance of different functional groups of coral reef sponges.

Variable affected	Phototrophic sponges	Heterotrophic sponges	Bioeroding sponges	References and notes
Particulate organic matter (POM) pool	—	—	—	Ribes et al. (2005), Lesser (2006)
Dissolved organic carbon (DOC) pool	?	—	—	de Goeij et al. (2008a, b), Mueller et al. (2014)
Inorganic nutrient pool				DIN (Southwell et al. 2008, Morganti et al. 2017)
N	+	+	+	P (Ribes et al. 2012)
P	+	+	+	Polyphosphate (Zhang et al. 2015)
Si	—	—	—	Si (López-Acosta et al. 2016)
Detritus	?	?	?	(Hadas et al. 2009, de Goeij et al. 2013, McMurray et al. 2018, Rix et al. 2016, Rix et al. 2018)
Spongivores	+	+	+	Guida (1976), Wulff (1994), Hill (1998), Wulff (2006), González-Rivero et al. (2012), Loh et al. (2015)
Mucus	+	+	+	Thompson et al. (1985), McGrath et al. (2017)
Space availability	—	—	—	Aronson et al. (2002), Schönberg and Ortiz (2008)
Primary production	+	N/A	+	Cheshire and Wilkinson (1991), Hill (1998)
Bioerosion	N/A	N/A	+	Schönberg and Ortiz (2008)
Habitat provision	+	+	—	Koukouras et al. (1996), Gratwicke and Speight (2005)
Reef consolidation	+	+	—	Wulff and Buss (1979), Biggs (2013)
Intra-specific competition	+	+	+	de Voogd et al. (2003)
Inter-specific competition	+	+	+	Fang et al. (2017)
Biomass of associated microorganisms	+	+	N	Ribeiro et al. (2003), Wulff (2006), Gloeckner et al. (2014)

Notes: Positive (+), Negative (—) and Neutral (N). DIN, Dissolved Inorganic Nitrogen; P, Phosphate; N/A, not applicable to this functional group; ?, more information is needed. Note that not all of the studies are from tropical environments and the table provides examples rather than a comprehensive review. Phototrophic sponges are those deriving a portion of their nutrition from photosynthetic symbionts, heterotrophic sponges are those primarily deriving their nutrition from suspension feeding, and bioeroding sponges are those that excavate substrate and can be either phototrophic or heterotrophic.

to cause changes to habitat complexity: while absolute increases in sponges may increase habitat complexity due to the complex range of sponge morphologies (Boury-Esnault and Rützler 1997), a relative increase in sponge abundance and decline in coral will likely result in a rapid loss of complexity (Luckhurst and Luckhurst 1978, McCormick 1994, Rogers et al. 2014), although no specific comparisons between sponge and coral-dominated systems have yet been made. Any such declines are likely to have flow-on effects to other trophic levels. For example, a reduction in fish refugia may make them more vulnerable to predators.

ASSESSING INDIRECT AND CASCADING EFFECTS OF CHANGING SPONGE DOMINANCE

While the direct effects of changing sponge dominance are relatively easy to quantify, it is much harder to predict the broader or indirect impacts on ecosystem function. The recent discovery that cryptic framework-dwelling sponges may play an important role in the recycling of dissolved organic carbon (DOC) to produce detritus, which is transferred to higher trophic levels through the “sponge loop” (de Goeij et al. 2013), is an example of the wider ecosystem-level linkages formed by sponges. However, the ubiquity of the sponge loop has not yet been established for non-cavity sponges (but see McMurray et al. [2018] who reported little evidence for the sponge loop in a number of Caribbean sponge species), and particularly for Indo-Pacific reefs, which tend to have a higher proportion of phototrophic species that are likely to be less reliant on DOM for nutrition (Wilkinson 1987). Furthermore, sponges also consume detritus (Hadas et al. 2009, McMurray et al. 2016), although it remains unclear if sponges are net consumers or producers of detritus.

Changes in sponge dominance may also affect higher trophic levels through spongivore activity, shifts in spatial interactions, and alterations to food availability for other suspension feeding organisms. There may also be wider impacts on fisheries productivity as a result of any alterations to trophic structure and changes to reef complexity and topography. In particular, sponge-mediated bioerosion directly impacts the ability of corals to maintain their calcium carbonate skeleton; consequently, bioerosion can have additional indirect effects by reducing structural complexity for macroorganisms (Glynn and Manzello 2015). Rugosity and diversity of coral growth forms are important drivers of fish abundance and diversity (Gratwicke and Speight 2005), hence destruction of carbonate reef structure by bioeroding sponges may exacerbate other stressors, ultimately resulting in declines in productivity of reef fisheries (Rogers et al. 2014). An increase in bioeroding sponges coupled with declining coral abundance also has the potential to alter reef carbon budgets (Glynn and Manzello 2015) and reef geomorphology, which will leave reefs with negative overall carbon budgets and a loss of reef structure and integrity. Ultimately such transitions would also lead to ecosystems that are no longer suitable for sponges if there is no primary carbonate structure on which they can attach. It is important to highlight that deeper water sponge-dominated assemblages do provide habitat complexity without any hard substratum and support extensive fisheries (Sainsbury et al.

1997). However, whether or not such sponge assemblages could persist in shallower waters remains unknown.

These examples demonstrate the complex indirect ways in which sponges are involved in ecosystem processes and the importance of exploring these effects for predicting future reef function.

MODELLING TO EXPLORE CHANGING RELATIVE SPONGE AND CORAL ABUNDANCE

To explore the indirect effects of (1) decreasing absolute coral abundance relative to sponge abundance and (2) increasing absolute sponge abundance relative to coral abundance, we created a compound qualitative model (see Appendix S1 for details on the modelling approach, model construction, and assumptions) for a simplified reef system. We included biological components to represent the major benthic and pelagic groups, as well as space and habitat complexity to represent the physical attributes of reef systems. The compound model was used to summarize the consequences of perturbations resulting from ocean warming (OW), ocean acidification (OA), and increased turbidity on different components of the system (Fig. 1). Extreme weather events are predicted to increase with global climate change (IPCC 2014), and these storms resuspend and re-distribute large amounts of sediments with impacts on marine invertebrates (AIMS 2017).

Qualitative models of coral reefs have previously been used to highlight key processes, evaluate sets of hypotheses, or generate new hypotheses. Some studies have focused on specific ecological groups and evaluated competing hypotheses; for example, Babcock et al. (2016) explored anthropogenic and environmental factors affecting crown-of-thorns starfish outbreaks on the Great Barrier Reef. Other studies have used qualitative models to represent coral reefs as sets of functional components and basic interactions and evaluated system responses to perturbations (Mumby and van Woesik 2014, Harborne et al. 2017). In general, as the complexity of a qualitative model increases, the outcomes become increasingly ambiguous (Dambacher et al. 2002). Hence, qualitative models are only used to consider the strongest interactions in the system and score them as either positive or negative. Due to the complexity and connectedness of our initial compound model, results were ambiguous for most taxa (Fig. 1, Table 2). However, increased OW, OA, and turbidity resulted most notably in unambiguous declines in coral abundance and habitat complexity. The uncertainty in how other benthic groups will respond stems from the complex interplay between climate-mediated stress, biotic interactions between taxa, and the uncertain effect of climate change on other reef system components (Harborne et al. 2017), with ambiguity in the responses of the benthos also propagating to upper trophic levels.

Due to the ambiguous response of many taxa, in particular sponges, in the initial compound model, and to further explore changes attributed to an increase in absolute sponge abundance relative to corals, or a reduction in absolute coral abundance relative to sponges, we created a series of simpler models. These simple models aimed to explicitly test the influence of habitat complexity and the sponge loop on reef function, as well as to explore different possible directions

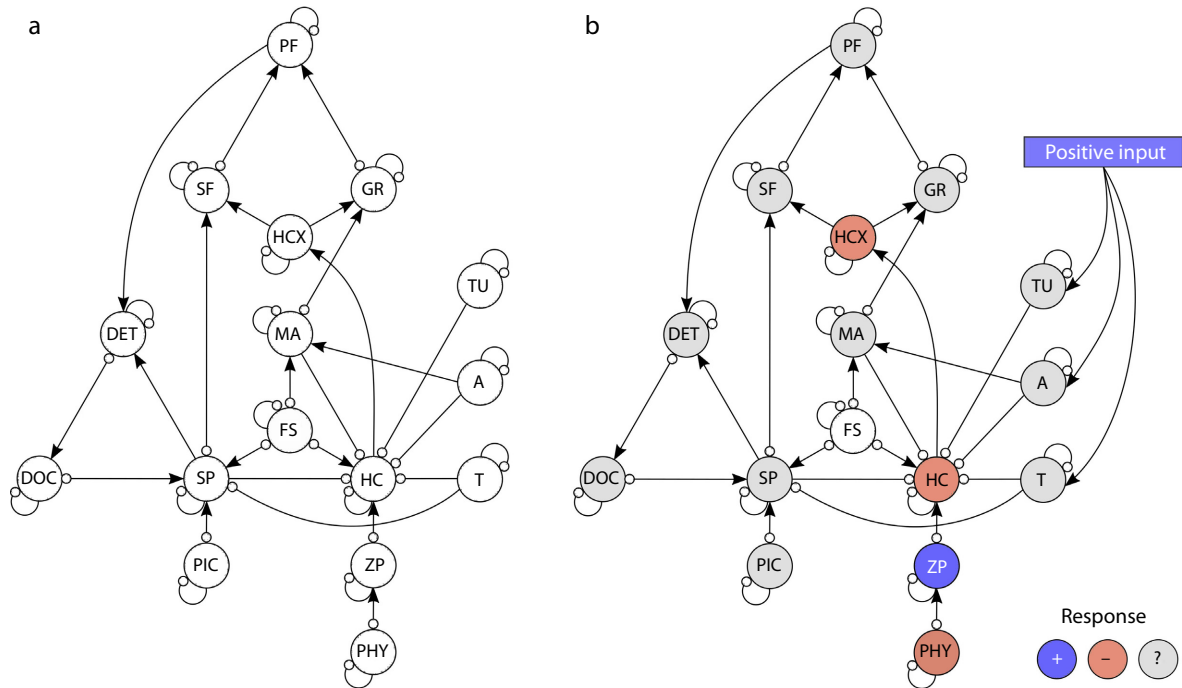


FIG. 1. (a) Qualitative model of a coral reef. In order from top to bottom: piscivorous fish (PF), spongivorous fish (SF), grazers (GR), habitat complexity (HCX), turbidity (TU), detritus (DET), macroalgae (MA), acidity (A), free space (FS), sponges (SP), hard corals (HC), temperature (T), picoplankton (PIC), zooplankton (ZP), phytoplankton (PHY). (b) Effects of a simultaneous increase in temperature, acidity, and turbidity as potential outcomes of climate change and human impact on coral reefs, with associated responses. The ends of the arrows indicate the effect of the source variable on the target variable, with (→) denoting a positive effect, (---) a negative effect, and (···) no effect. Free space was incorporated in the model as a state variable in order to explicitly represent passive occupation of the substrate, alongside specific interactions between benthic groups. However, increases or decreases in free space were not reported as model results because fluctuations in free space would be difficult to interpret in the context of three benthic groups competing for it.

TABLE 2. Response of the modeled functional groups to the applied press perturbations (first row).

Perturbation applied	Compound model ↑ Temperature, acidity, turbidity	Core model		Habitat complexity model		Sponge loop model		Macroalgal dominance model	
		↓ Hard corals	↑ Sponges	↓ Hard corals	↑ Sponges	↓ Hard corals	↑ Sponges	↓ Hard corals	↑ Macroalgae
Sponges	?	+(1)	+(0.7)	+(0.5)	?	+(1)	+(0.7)	?	?
Hard corals	-(0.53)	-(1)	-(0.67)	-(1)	-(0.67)	-(0.7)	-(0.67)	-(0.81)	?
Macroalgae	?	+(1)	?	+(0.55)	?	+(0.68)	?	+(1)	+(0.78)
Spongivorous fish	?	?	+(0.6)	?	?	?	+(0.6)	?	-(0.66)
Grazers	?	+(0.67)	?	?	?	?	?	+(0.71)	+(0.73)
Piscivorous fish	?	+(1)	+(0.5)	-(0.55)	?	+(0.83)	+(0.5)	+(0.67)	?
Picoplankton	?	-(1)	-(0.7)	-(0.5)	?	-(1)	-(0.7)	?	?
Zooplankton	+(0.53)	+(1)	+(0.67)	+(1)	+(0.67)	+(0.71)	+(0.67)	+(0.81)	?
Phytoplankton	-(0.53)	-(1)	-(0.67)	-(1)	-(0.67)	-(0.71)	-(0.67)	-(0.81)	?
Habitat complexity	-(0.53)			-(1)	-(0.67)				
Detritus	?					+(1)	+(0.66)		
Dissolved organic carbon (DOC)	?					?	?		

Notes: Responses are positive (+), negative (-), or ambiguous (?). For unambiguous responses, the weighted prediction (*W*) is indicated. *W* ranges from 0 to 1, with *W* = 0 corresponding to complete ambiguity and *W* = 1 to complete certainty. A prediction weight of *W* ≥ 0.5 has been found to correspond to >90% correct predictions (Dambacher et al. 2003; see also Appendix S1).

of competitive interactions between sponges and macroalgae, which are poorly understood (Wulff 2006). For this purpose we first built a simplified “core” model (Fig. 2a) without OW, OA, and turbidity and represented these perturbations in the model as a decline in corals. This has the advantage of reducing system complexity, thus allowing for a better understanding of how increases or decreases in

certain taxa affect the rest of the community. The exclusion of climatic variables from the core model and the direct application of a negative press perturbation on corals was supported by the unambiguous decline of corals in the compound model as a result of OW, OA, and turbidity. This core model also excluded habitat complexity and the sponge loop, but it overall maintained the same dynamics as the

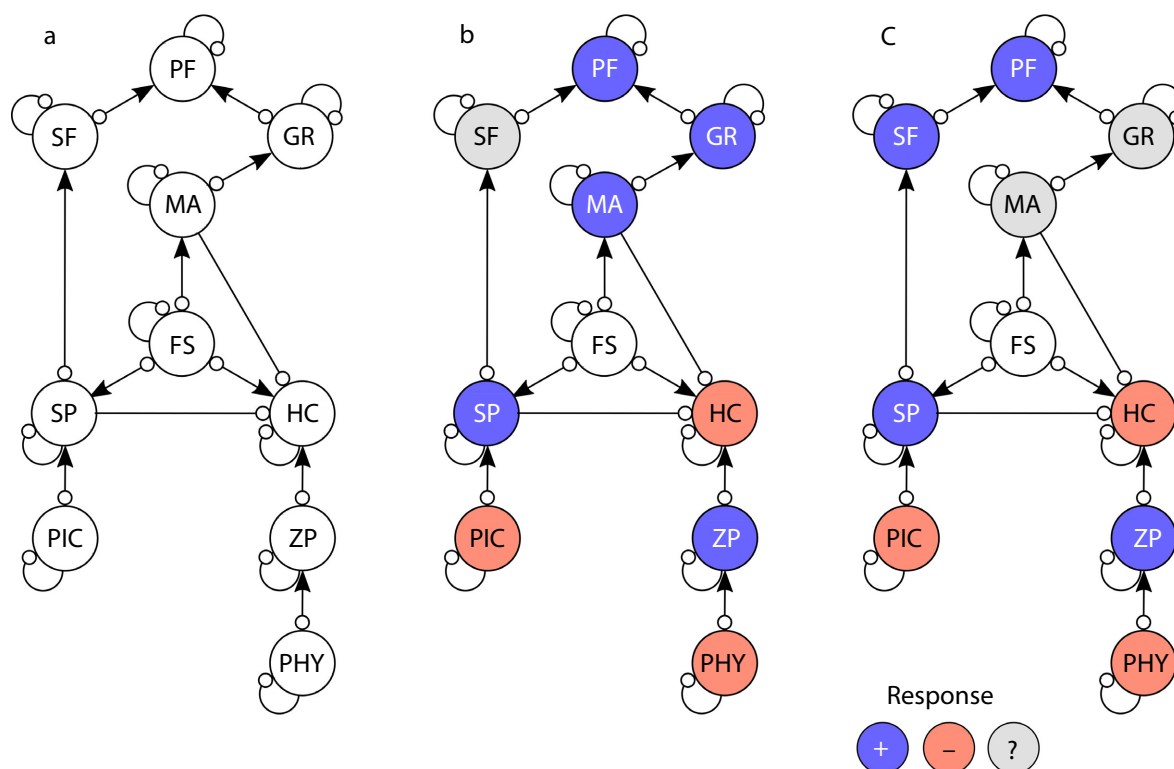


FIG. 2. (a) Core model derived from the model shown in Fig. 1. (b) Perturbation provides a negative input on corals. (c) Perturbation provides a positive input on sponges. In order from top to bottom: piscivorous fish (PF), spongivorous fish (SF), grazers (GR), macroalgae (MA), free space (FS), sponges (SP), hard corals (HC), picoplankton (PIC), zooplankton (ZP), phytoplankton (PHY). The ends of the arrows indicate the effect of the source variable on the target variable, with (→) denoting a positive effect, (—○) a negative effect, and (—) no effect.

compound model. We first considered the impact of either a decline in corals (Fig. 2b) or an increase in sponge abundance (Fig. 2c) on the core model. Predictions from these core models were generally unambiguous, irrespective of whether coral abundance declined or sponge abundance increased. Declining coral abundance resulted in a predicted increase in sponges and macroalgae, a decrease in picoplankton as a result of sponge feeding, and a higher abundance of grazers, which supported higher trophic levels (Fig. 2b). When sponge abundance was increased, the predictions from the core model were similar except that the outcome for macroalgae became ambiguous (Fig. 2c). To test hypotheses about the relative importance of habitat complexity and the sponge loop we then added both components into the core model, resulting in two intermediate models (Fig. 3). For the habitat complexity model (Fig. 3a–c), a reduction in coral abundance produced similar outcomes to the core model, except that piscivorous fish were predicted to unambiguously decrease (Fig. 3b). In contrast, with increased sponge abundance, the responses of other components of the model became largely ambiguous, including the response of sponges themselves, with the exception of habitat complexity and coral abundance, which both unequivocally decreased (Fig. 3c). When coral abundance was reduced for the model incorporating the sponge loop, sponge and algal abundances both increased, although the response of spongivores became ambiguous (Fig. 3e). When sponge abundance was increased for the model incorporating the sponge loop, there were few differences

compared to the core model (Fig. 3f). Notably, piscivorous fish were predicted to increase in both models incorporating the sponge loop, likely due to the trophic pathway created from the production of detritus.

WHAT MIGHT A CHANGE IN SPONGE DOMINANCE MEAN FOR REEF ECOSYSTEM FUNCTIONING?

Despite the simplicity of our models, ecosystem-level responses predicted from decreasing coral abundance relative to sponge abundance clearly differ from those of increasing absolute sponge abundance. Habitat complexity is strongly linked to reef diversity and productivity (Rogers et al. 2014), hence it is not surprising that the abundance of piscivorous fish declines in conjunction with declining coral abundance in the model incorporating habitat complexity. However, when sponge abundance was increased relative to corals, the model became far more uncertain, and the impact on the highest trophic level (piscivorous fish) was ambiguous. Notably, when we evaluated system responses to a decline in corals in the model with the sponge loop, model predictions included an increase in abundance of piscivorous fish, despite ambiguous responses of spongivores and grazers (Fig. 3e). The positive response by the highest trophic level is likely driven by an increase in low-trophic-level edible biomass represented by macroalgae and sponges, with the latter being sustained by the detrital loop. Given the potential for the sponge loop to support higher trophic levels through the conversion of DOM into detritus or sponge biomass that become food for

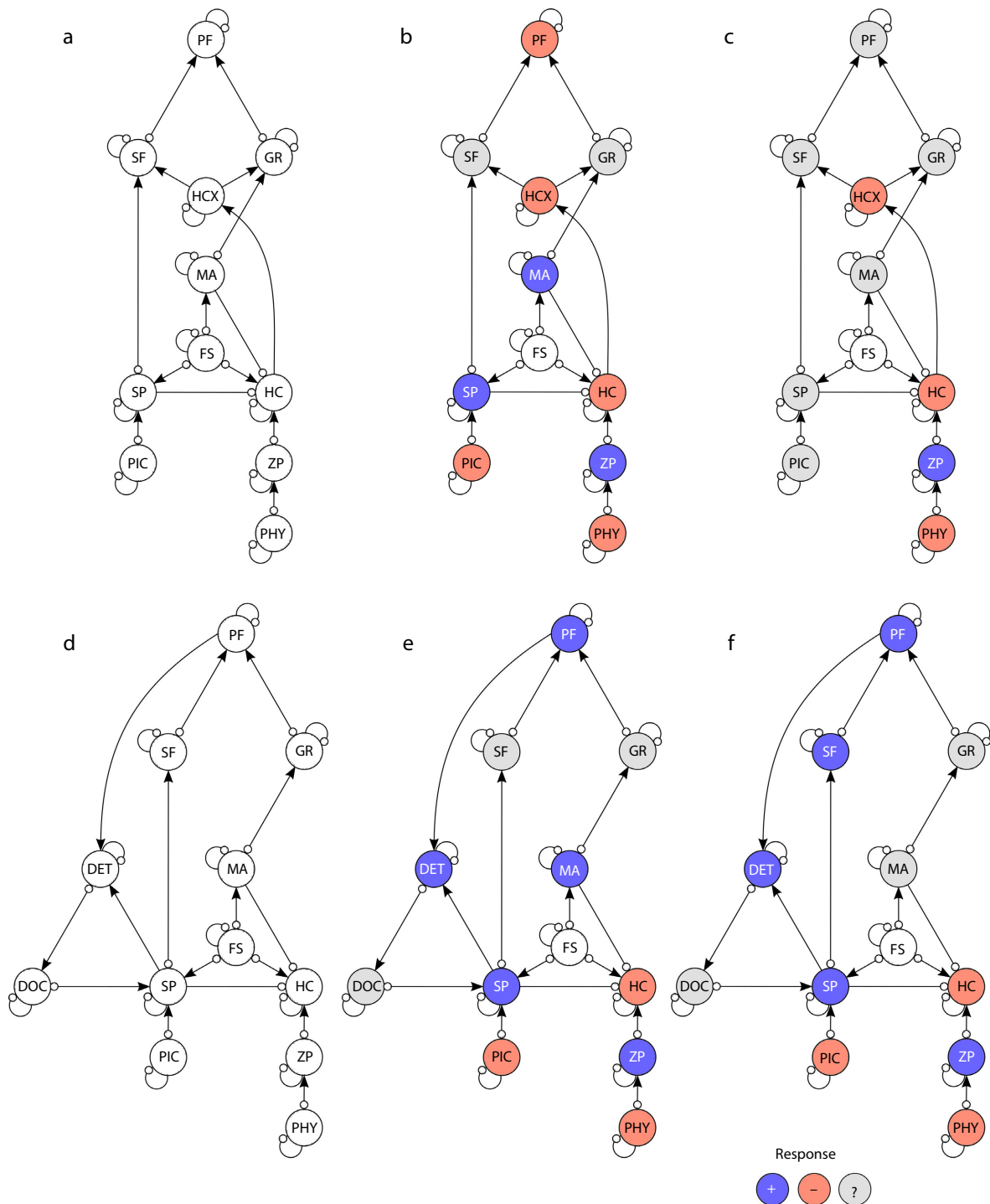


FIG. 3. Qualitative models of a coral reef incorporating (a–c) habitat complexity and (d–f) the sponge loop. Panels b and e show the response of each system to negative press perturbation acting on corals whereas c and f show a positive press perturbation acting on sponges. In order from top to bottom: piscivorous fish (PF), spongivorous fish (SF), grazers (GR), habitat complexity (HCX), macroalgae (MA), free space (FS), sponges (SP), hard corals (HC), picoplankton (PIC), zooplankton (ZP), phytoplankton (PHY), detritus (DET), dissolved organic carbon (DOC). The ends of the arrows indicate the effect of the source variable on the target variable, with (→) denoting a positive effect, (—○) a negative effect, and (—) no effect.

reef consumers (McMurray et al. 2018, Rix et al. 2018), there is clearly a need to understand the importance of the sponge loop for reef ecosystems globally, particularly if the ubiquity of this pathway varies between regions and amongst species (McMurray et al. 2018).

A key emergent question is whether higher trophic levels can be supported through the sponge loop on reefs with lower habitat complexity. Given the demonstrated relationship between diversity and habitat complexity on reefs (Rogers et al. 2014), it seems counterintuitive to expect all

higher trophic levels to be supported by sponge reefs unless greater sponge abundance can maintain some level of habitat complexity. Fortunately, sponge morphologies can be highly complex, and many deeper-water reefs are already dominated by sponges (Lesser et al. 2009), which appear to provide the necessary habitat for diverse reef-associated fauna (Kahng et al. 2014).

ALGAL REEFS VS. SPONGE REEFS

Algae are expected to directly benefit from OA and declining coral abundance, with many regime shifts to algal-dominated systems already evident (Bruno et al. 2009). If sponges also tolerate OA conditions, spatial competition between algae and sponges will be inevitable. However, with the exception of bioeroding Clionids (González-Rivero et al. 2011, 2012, 2016), competitive interactions between sponges and algae on coral reefs are largely unknown (Wulff 2006), since these interactions are generally rare on unaltered reefs. Previous modelling in the Caribbean has suggested that bioeroding sponges may dissipate algal grazing pressure by providing generalist fish with an alternative food source (González-Rivero et al. 2011). More recently, González-Rivero et al. (2016) found that macroalgae, which had fast colonization rates and superior competitiveness, prevented bioeroding sponges from becoming dominant following coral declines in the Caribbean. Looking forward, it will be imperative to address uncertainty in the outcomes of

competitive interactions between non-bioeroding sponges and algae, particularly in regions where they co-occur in high abundance. Furthermore, it will be important to address the role of microbes in these competitive interactions, since recent studies have identified the important roles played by microorganisms in mediating coral-algal interactions (Roach et al. 2017).

To represent the consequences of a competitive interaction where algae limit sponge abundance or growth, and to determine how increased algal abundance impacts the system, we created an additional core model that captures a negative impact of macroalgae on sponges (Fig. 4a). When a decline in coral abundance was applied to this core model, sponges were predicted to respond ambiguously whereas algae and grazers responded positively (Fig. 4b). The ambiguous response of sponges, their predators, and their food source highlights the current lack of knowledge about sponge dynamics, and sponge interactions resulting from coral to algae regime shifts. Given this ambiguous sponge response, we tested for the response of the system to a positive input on macroalgae (increased abundance) instead of sponges. This second press perturbation resulted in mostly ambiguous model predictions across the system (Fig. 4c). The ambiguous outcomes from these models further highlight the critical need to advance our understanding of competitive relationships between macroalgae and sponges, and how such outcomes resolve when coral abundance is reduced.

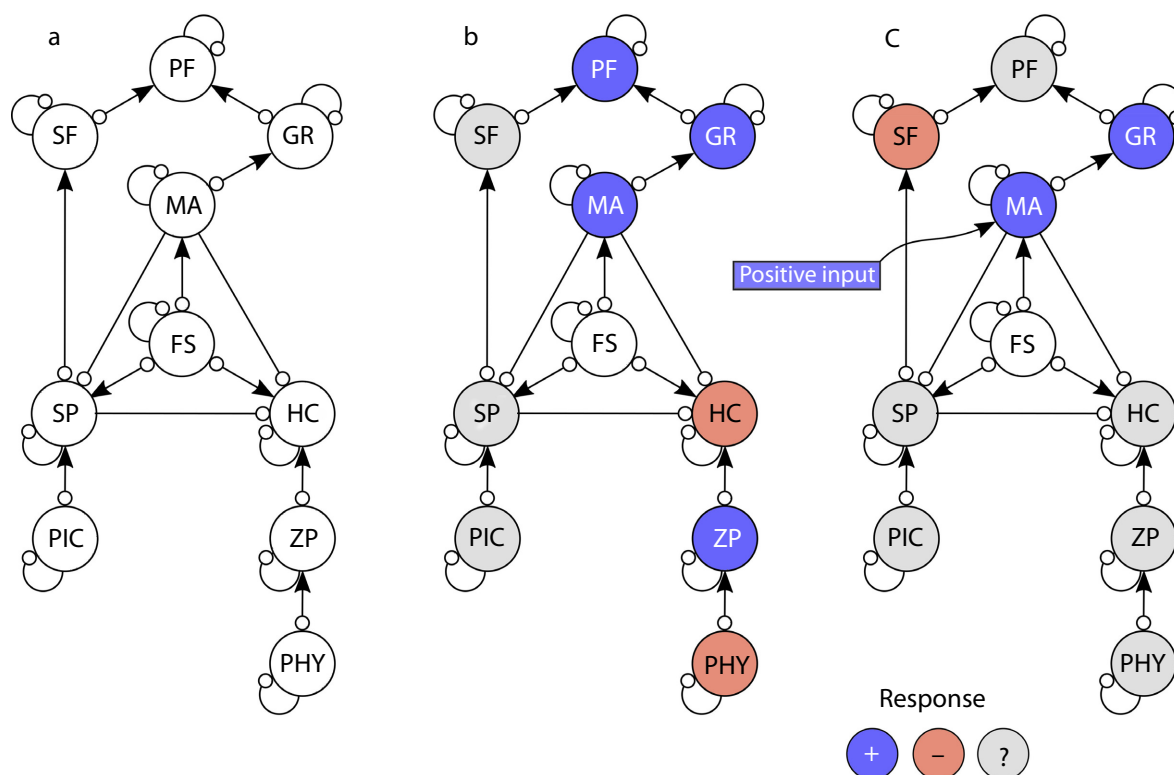


FIG. 4. (a) Core model derived from the model shown in Fig. 1 including the negative interaction of algae on sponges. (b) Perturbation provides a negative input on corals. (c) Perturbation provides a positive input on algae. In order from top to bottom: piscivorous fish (PF), spongivorous fish (SF), grazers (GR), macroalgae (MA), free space (FS), sponges (SP), hard corals (HC), picoplankton (PIC), zooplankton (ZP), phytoplankton (PHY). The ends of the arrows indicate the effect of the source variable on the target variable, with (→) a positive effect, (—○) a negative effect, and (—) no effect.

HOW MIGHT OTHER CHANGES ON REEFS DIRECTLY OR INDIRECTLY INFLUENCE SPONGES?

Here we have focused on sponges as a primary filter-feeding taxon, but other groups will also respond to OA, OW, and turbidity increases in ways that we have not captured in our simple qualitative models. Nevertheless, these responses also have the potential to impact sponges either directly or indirectly. In particular, there has been recent interest in the “microbialization” of coral reefs, which refers to a shift in ecosystem trophic structure toward higher microbial biomass and energy use (Haas et al. 2016). Given that sponges feed on heterotrophic bacteria (Lesser 2006), such changes would likely provide increased or alternative food resources to sponges. Although sponges will be in competition with algae, sponges also have the potential to benefit from increases in macroalgae, either directly through the consumption of greater amounts of DOC produced by the algae, or through the consumption of bacteria, which are thought to be utilizing the DOC on algal-dominated reefs (Haas et al. 2016). Similarly, the mucus produced by corals and other benthic organisms (Silveira et al. 2017), which is released to the surrounding environment, can be consumed by sponges (Rix et al. 2016, 2018), and is also a carbon source for microbes, upon which sponges can subsequently feed. The strength of these effects will depend on whether DOC and particulate organic carbon (POC) as carbon sources for sponges are limiting on reefs; this is currently unknown.

It is important to note that sponges support a wide diversity of microbial and macrofaunal symbionts, and that the functional basis of these relationships is only just starting to be elucidated. Degraded environments are often dominated by only a few tolerant sponge species (Powell et al. 2014, Knapp et al. 2016), hence sponge-associated organisms will also likely show variation in their tolerance to stressors. While we already have some understanding of how sponge-associated microbial communities respond to OW, OA, and elevated sediments (Fan et al. 2013, Morrow et al. 2015, Webster et al. 2016, Pineda et al. 2017a, b), there is still a major knowledge gap about how sponge-associated macrofauna respond to these environmental pressures and how this impacts host health and fitness.

HOW MIGHT A SPONGE REEF FUNCTION?

Sponge dominated reefs will function differently to current coral dominated reefs (see Bell et al. 2013 for initial discussion of this topic), although the nature and strength of the divergence will depend on whether sponge dominance occurs as a result of increased sponge abundance or declining coral abundance. The primary difference is expected to be an overall loss of biodiversity in sponge dominated systems, largely as a result of declining habitat complexity, and a change in benthic-pelagic relationships, both of which will reduce food availability to higher trophic levels. It is also highly likely that reefs would transition into a negative calcium carbonate accretion state.

A transition to sponge-dominance would cause the benthic community to shift from being primarily comprised of phototrophic organisms to being dominated by predominately

heterotrophic species. Initially, this would impact those organisms that are obligate coral feeders (Pratchett et al. 2006) or taxa that rely on coral derived DOC (Wild et al. 2004), although it is possible that these species could acclimatize to utilize DOC from increased macroalgal production. Being highly efficient suspension feeders, changes in sponge dominance through increased absolute abundance may also deplete the bacterioplankton, with foreseeable negative consequences for less efficient filter feeders. Increased sponge abundance would also require greater quantities of DOC (McMurray et al. 2017), although reliance of sponges on DOC varies between species (Hoer et al. 2018), so we may see major changes to sponge population structures.

Habitat complexity would be lower on a sponge dominated reef due to a reduction in the intricate branching structures that are characteristic of corals but less evident in sponges. Loss of habitat complexity has a number of negative ecological feedbacks as it reduces the habitat available for juvenile fish to hide from predators, which in turn reduces diversity and overall productivity of lower trophic levels. Sponge dominated reefs would predominantly provide habitat for generalist fish species and spongivores, (Wulff 2006), reducing the complexity of the food web and resulting in a reef that is less resilient to further anthropogenic impact.

A sponge-dominated reef is unlikely to be a long-term state since sponges are not producing calcium carbonate (with the exception of small amounts by calcareous sponges) to enable reef accretion. While there was some thought that bioeroding sponges could tolerate ocean warming (Fang et al. 2014), recent work has shown that *Cliona* has not increased on inshore reefs over the past decade (Ramsby et al. 2017) and cannot survive ocean temperatures projected for 2100 (Achlati et al. 2017, Ramsby et al. 2018), therefore they will have a negligible impact on reef erosion or function. Importantly, since sponges require hard substrate for settlement and stability, they are not likely to persist if the primary reef structure has entirely broken down. It is difficult to estimate how long it might take for the reef structure to breakdown to a stage where epilithic sponges can no longer colonize reefs, but it seems unlikely to be more than a few hundred years.

REGIONAL VARIATION IN SPONGE REEF FUNCTION

The functional attributes of sponge-dominated reef ecosystems are likely to vary between different geographic regions. In particular, the Indo-Pacific is thought to contain a higher proportion of phototrophic species, whereas the Caribbean contains a higher proportion of heterotrophic species (Wilkinson 1987). However, the ubiquity of this generalized pattern still needs to be tested for more reef systems, as the mode of nutrition will strongly impact sponge-water column interactions. In particular, phototrophic species are less reliant on externally acquired DOC and POC as carbon sources and may contribute less to the sponge loop. In addition, there appears to be regional variation in the regime shifts reported on coral reefs that might influence sponges. Specifically, while many recent regime shifts have involved transitions from coral- to algal-dominated reefs, the majority of these have

occurred in the Caribbean (Bruno et al. 2009). While the basis for this regional variability is not well understood and may simply reflect the much lower overall coral cover in the Caribbean (Gardner et al. 2003, Bruno and Selig 2007, De'ath et al. 2012), if coral declines do not result in higher algal abundance then this would likely have direct impacts on sponges through reduced spatial competition and lower DOC availability.

ADDRESSING THE UNCERTAINTY OF A SPONGE-DOMINATED REEF

While we have identified a number of important research questions that need to be addressed in order to advance our understanding of how sponge-dominated reefs might function (Box 1), answering these questions is not trivial. The ubiquity of the sponge-loop and potential for this pathway to support the highest trophic levels needs further focus, and although data for a wider range of species is starting to become available (McMurray et al. 2018), we encourage the coral reef community to examine a much broader suite of species across different reef habitats and geographic regions. There is also a need to explicitly track the movement of carbon through the food chain, since demonstrating the conversion of carbon to sponge-derived detritus does not in itself link sponges to the highest trophic levels. Important questions also still remain regarding the role of detritus in sponge carbon flow, especially considering that detritus is both produced and consumed by sponges (Hadas et al. 2009). Controlled field experiments using labelled carbon are therefore needed to track the long-term fate of sponge-derived detritus.

The extent of changes to habitat complexity with increasing sponge dominance also warrants further consideration. This could be achieved in part, through comparisons of fish assemblages associated with already sponge-dominated habitats, such as those reported from shallow waters in Timor Leste (Farnham and Bell 2018) and the Wakatobi (Powell et al. 2014). Mesophotic reefs may also offer considerable insight into how a sponge-dominated reef might function (Kahng et al. 2010). Experimental research that

re-creates the level of habitat complexity afforded by sponges, for example using three-dimensional printed surfaces, would also yield valuable insights into the function of sponge dominated systems.

Quantitative rate data for sponge depletion of (bacterio)-plankton is needed to reveal the broader ecosystem consequences of increased sponge abundance and to determine whether sponges are likely to be limited by food availability. This data would also strengthen our prediction that sponges could benefit from increased macroalgal derived DOC or from increased bacterioplankton resulting from reef microbialization. While recent research has shown that sponges can take up coral derived DOC (Rix et al. 2018), it seems unlikely that they are discriminating between different DOC sources, so declines in coral DOC could potentially be met by increases in macroalgal DOC. Understanding these relationships requires a research focus on carbon assimilation at the sponge assemblage level, rather than at the individual species level (Perea-Blazquez et al. 2012). Given the complexities of these feeding interactions and their potential to propagate in unpredictable ways through ecosystems, trophic and whole-ecosystem models would be a useful way to explore these relationships.

Given that coral-algal regime shifts have been reported across the world (Hughes et al. 2007), the spatial relationships between sponges and algae needs further investigation. Sponges are rarely mentioned in studies where coral reefs have transitioned to algal-dominated reefs (e.g., Hughes et al. 2007 only reports changes in coral and algal abundance) but given the general resilience of sponges to anthropogenic disturbance, it is likely that sponges have persisted despite the coral declines. Controlled experiments and in situ manipulations would further elucidate the competitive relationships between algae and sponges, and help determine if sponges can persist in algal-dominated ecosystems.

CONCLUSION

It is not our intention to suggest that all reefs will transition to sponge-dominated systems. However, there is increasing evidence to suggest that many coral reef sponges are more resilient to environmental change than corals (Bell et al. 2013, Bennett et al. 2017). Further declines in coral abundance or direct increases in sponge abundance as a result of increased productivity (Bennett et al. 2017) or increased DOC/POC availability will have significant impacts on other ecosystem components. Our models provide the first insights into how sponge-dominated reefs might function and the likely outcomes from increasing absolute vs. relative sponge abundance. Addressing the key knowledge gaps identified here (see Box 1 for summary) will provide the foundation for further complex models that reliably predict the outcomes of changing sponge dominance for ecosystem service provision. Finally, the research priorities identified by our modelling are relevant for other ecosystems where major changes in the dominant organisms are expected as a result of climate change.

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Box 1. Priority research questions

- How widespread is the sponge loop in tropical environments, particularly across the Indo-Pacific?
- Can carbon from the sponge loop support higher trophic levels where overall habitat complexity is reduced?
- How will structural complexity change as coral reefs transition to sponge-dominated reefs?
- How limiting are current carbon sources to reef sponges, and how will reductions in coral mucus and increases in DOC from macroalgae influence sponges?
- Are sponges net consumers or producers of detritus?
- Can sponges benefit from the microbialization of coral reefs?
- What are the outcomes of spatial interactions between sponges and algae, and how are such outcomes mediated?

Rovellini designed the study. A. Rovellini performed the modeling work and analyzed the output data. S. K. Davy, M. W. Taylor, H. M. Luter, E. A. Fulton, M. R. Dunn, H. M. Bennett, and N. M. Kandler contributed to interpretation of the data. J. J. Bell and N. S. Webster wrote the first draft of the manuscript and all authors contributed to revisions and approved the manuscript.

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SUPPORTING INFORMATION

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